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Abstract:	

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Abstract

Social traditions, here defined as displaying inter-group behavioural differences acquired through social learning, have been identified in a number of primate species. Here we review research methods used in the wild and in captivity to identify the presence of both primate social traditions and the necessary social learning mechanisms involved. Moving beyond evidence of the presence of primate social traditions, to their function, longevity, biased transmission, conformity and cumulative nature, allows for the exploration of convergences and divergences between primate and human traditions.

Keywords

Tradition, learning, transmission biases, conformity, cumulative culture.

A social tradition is a *distinctive* and *persistent* behavioural trait shared by several members of a group. Critically, the spread of this behavioural trait is facilitated by *social learning* from one individual to another. Social traditions are not unique to humans and several other primate species demonstrate social traditions, from food processing to social conventions. This article offers an overview of how differing research methods have illuminated the vast array of primate social traditions. Underpinning these traditions are a suite of social learning mechanisms that we summarise and discuss. Moving beyond descriptions of traditions to the identification of variable features such as the function, longevity, selective transmission, and, at times, cumulative nature of primate traditions will highlight convergences and divergences between primate traditions and human culture.

Identifying Social Traditions

Varied research methods, including systematic observation, experimental studies and social network analyses, have identified a number of primate social traditions (see Whiten, 2012 for a detailed review of methods and studies). One primary method of identifying social traditions within a species is to observe inter-group differences in the behavioural repertoire of the same species. This can be achieved through a collaborative amalgamation of observations at multiple field sites. Comparisons of these observations can highlight behaviour patterns that are common for at least one community yet absent for another, with no discernible genetic or environmental explanation.

Such research has been undertaken with two ape species; orang-utans (*Pongo* spp.) and chimpanzees (*Pan troglodytes*). The results demonstrated 30 and 40 such behaviour patterns or traditions respectively, that were habitual in some communities but non-existent in others. For example, use of natural wooden and stone hammer materials to crack open hard nuts is customary in chimpanzee communities over a wide span of far-West Africa, yet

absent elsewhere despite the presence of all the raw materials confirmed in separate studies. Recent studies have even demonstrated differences in hammer type preferences in neighbouring communities, making alternatives explanations like genetic or ecological differences, implausible.

The large-scale data sets relating to inter-group behavioural differences are importantly complemented by recording a group's acquisition of a tradition 'as it happens'. Hobaiter et al. (2014) tracked the group spread of a moss-sponge drinking innovation by a dominant male chimpanzee while also studying the social dynamics within the community through the use of social network analysis. Social network analysis maps the strength of relationships between group members. Dynamic network-based diffusion analysis, which quantifies the extent to which the spread of a new behaviour is consistent with a *repeatedly* updated social network, led to the discovery that each time a novice observed an existing moss-sponger there was a 15-fold enhancement of moss sponging behaviour for that observer. These findings are valuable evidence of group traditions in chimpanzees, although purely observational studies of natural behaviour are correlational and care is necessary in inferring causation in such approaches.

Moving beyond observation and correlation to controlled experimentation which can reliably identify causation can further our understanding of primate social traditions. Target behaviours may be artificially created (by training models), seeded and manipulated in order to examine whether the seeded behaviour transmits across the group and, if so, the mechanisms of this transfer. Triangulating experimental manipulations of behaviours with observations allows for an even more detailed description. Claidiere, Messer, Hoppitt., & Whiten (2013) seeded foraging behaviours in two groups of squirrel monkeys housed in identical enclosures within a zoo. The alpha male in each group was trained to remove food from a puzzle using one of two different methods. The males then demonstrated their

respective method to the rest of the group, after which all members of the group had access to the task. Additionally, each monkey's total time spent in the experimental zone was coded dependent on whether they were alone or with specific conspecifics. This created a social network analysis where the network centrality of an individual, which increases with the strength of its social connections, was calculated. Results showed that the two techniques spread preferentially in the groups in which they were initially seeded. Furthermore, network centrality predicted both the speed with which an individual would first succeed in opening the artificial fruit and the probability that they would acquire the method seeded in their group (see Figure 1). These findings demonstrate how important social relationships can be in the spread of social traditions.

These various research methods demonstrate that (1) there are enduring group differences in behaviours among some wild populations of primates; (2) experimentally seeded behaviours can spread among a group creating micro-traditions; and (3) there is a relationship between social dynamics and social learning. We now focus on how behaviours may spread to create traditions by focussing on social learning mechanisms.

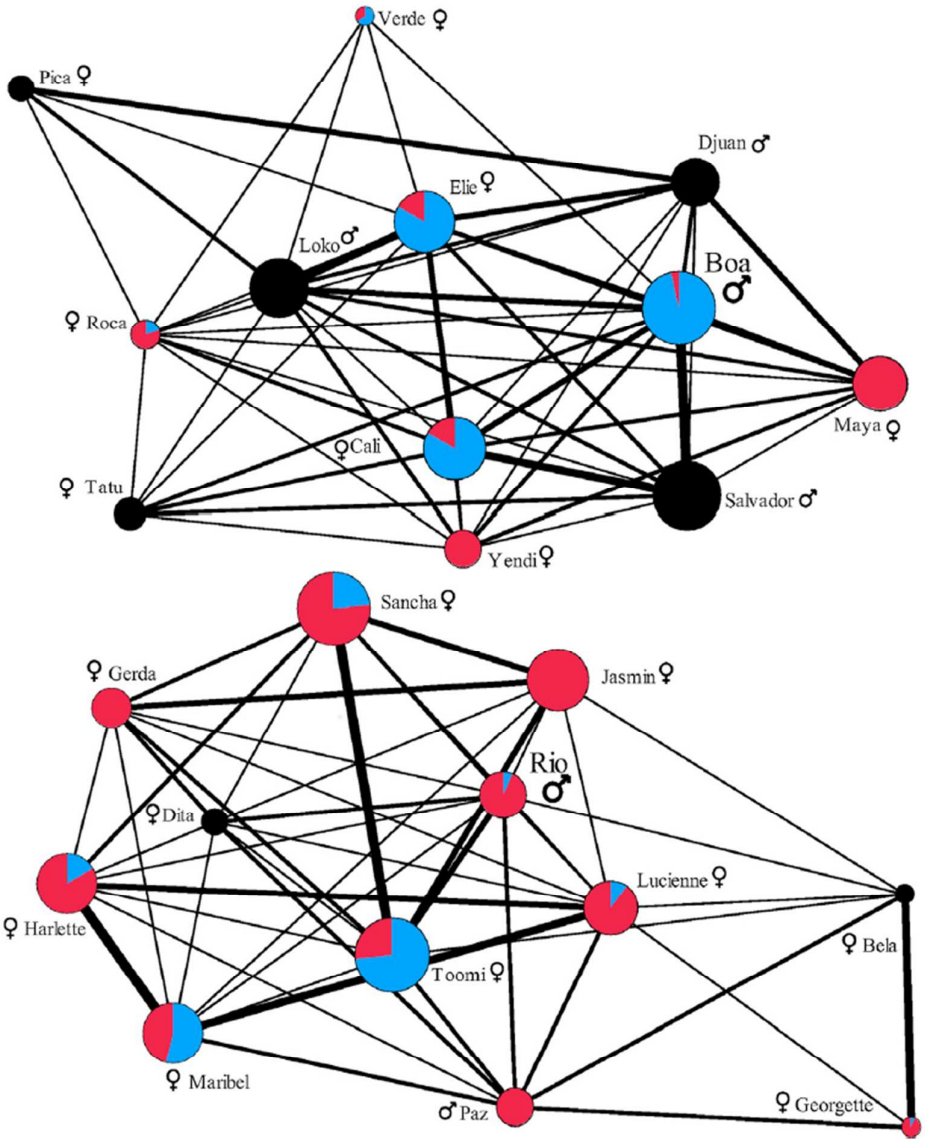

Fig. 1. Sociograms illustrating cultural diffusion in two groups of squirrel monkeys. Boa (top) was trained to use foraging method 1 (blue) and Rio was trained to use method 2 (pink). Link size is proportional to bond strength. Node size is proportional to the network centrality. Node colour indicates the actions performed by each monkey: the pie chart represents the proportion of method 1 (blue) and method 2 (red) for a maximum of 30 successes: a black node represents individuals that were unsuccessful. Figure reproduced from Claidiere et al. (2013)

98

99 **Social Learning Mechanisms**

100 By definition, social traditions rely on social learning; learning by observation of
101 another individual or its products. How this learning happens can vary dramatically both
102 within and between species. Identifying the mechanisms involved in social learning through
103 observing wild populations is challenging because shared behaviour among individuals does
104 not necessarily imply social learning and observation does not identify exactly *how*
105 behaviours may have been socially learned. Thus, experiments have proved a more fruitful
106 avenue of research. These experiments tend to focus on the use of artificially seeded
107 behaviour as with the captive squirrel monkeys described above (Claidiere et al., 2013).
108 Researchers can create artificial challenges involving the acquisition of food, akin to
109 accessing fruit within a natural shell ('artificial-fruit' tasks). Typically, an individual will
110 learn by exploration, or be trained, to access the food using a particular method, while an
111 alternative method is blocked. This individual then performs the behaviour in the presence of
112 one (dyadic approach) or more ('open' diffusion approach) individuals over a period of time.
113 Critically, scientists can then look beyond simple measures such as success or failure in
114 acquiring the food and look at the specific acquisition methods.

115 These social learning experiments have been conducted successfully with an ever-
116 growing number of primate species both in the wild and captivity, using a range of methods
117 (dyads, chains of dyads and open-diffusion), observational methods (live and video) and
118 different tasks. While these studies might not necessarily demonstrate the *persistence* of
119 behaviour required in traditions they shed light on the process of social learning. For
120 example, open-diffusion artificial-fruit experiments with humans, chimpanzees, vervet
121 monkeys, capuchins, marmosets, squirrel monkeys and lemurs (see Schnoell et al, 2014 for
122 the latter example) have shown that different groups, seeded with different methods of

123 extracting rewards, will show a group-level preference for the seeded method. Thus, these
124 species demonstrate the cognitive skills and social learning mechanisms necessary to sustain
125 social traditions across different communities, including quite complex variations in foraging
126 techniques.

127 These kinds of experiments can be extended to shed further light on learning
128 mechanisms. For example, an experimenter can manipulate the task by some hidden means,
129 resulting in the same task movement as with a live model. This 'ghost' control method allows
130 for a distinction between object or body movement re-enactment. If a species copies a
131 method equally well with or without a model then it may be that they are socially learning
132 through 'object movement re-enactment', but this says nothing of whether they can copy
133 another's actions towards a task. When a task is relatively easy, chimpanzees will initially
134 copy the extraction method, whether demonstrated by a model or a 'ghost' wire pulled by the
135 experimenter. However, fidelity to this method is much higher when a model demonstrates
136 the method. Furthermore, with a harder task, chimpanzees were unable to learn an artificial-
137 fruits retrieval method through a ghost display even though they could when modelled by a
138 conspecific (Hopper et al., 2008). This suggests that the presence and specific movements of
139 a model are important to the observer and suggests body movement re-enactment, or
140 imitation, is present in chimpanzees. However, it has been argued that primates tend to copy
141 only some aspects of a given behaviour, and precise information regarding actions is not so
142 readily transmitted, leading to cultural 'slippage'. In contrast, from a very young age humans
143 tend to copy actions, end results, and goals and show much higher fidelity copying, at times
144 resulting in the persistent copying of causally irrelevant or inefficient actions. Humans,
145 however, are not the only species that socially learn behaviours with opaque functions, as
146 explained in the following section.
147

Functions of Social Learning

In research on human copying, a distinction has been made between copying to learn new skills or deal with the physical environment (informative or instrumental context), and copying that might serve a social function (normative context). This difference could lead to two quite different types of social traditions. Thus, while the function of some copying might be to identify useful information about the environment, the function of normative cases might be to align oneself with a behaviour shared socially by a group, which in turn may serves the function of facilitating social relationships.

Thus far we have cited examples of primate social traditions that have an obvious function; methods of handling or acquiring food or water. Such social traditions have an obvious evolutionary advantage for individuals who can thus benefit from the innovations of group members, potentially innovations created many generations before. Indeed, 19 of 40 examples of social traditions found in the wild chimpanzees related to food or drink handling or acquisition. Other social traditions identified also had a relatively obvious advantage, such as one group's habitual behaviour of placing large leaves on the ground for sitting on, as an apparent protection from the wet ground. These social traditions can serve to inform naïve individuals about their physical environment.

Conversely, other social traditions identified in the chimpanzee groups did not inform individuals about the physical environment and thus have a more opaque function. For example, the same group of leaf-sitting chimpanzees showed a distinct method of grooming whereby the two grooming individuals clasped hands overhead and groomed each other with the other hand. While grooming behaviour is species-typical and is thought to strengthen social bonds, the specific style of the clasped hands seems arbitrary. This hand-clasp tradition was absent in other groups although these groups also possessed intra-group behaviours with less obvious functions. Inter-group differences in social interaction seem akin to human

cross-cultural differences in conventions like greetings involving handshakes, cheek kissing, bowing and embracing. Thus these traditions may have a normative rather than informational function.

Apes are not alone in demonstrating social traditions that do not function to improve interactions with the physical environment. Groups of Japanese macaques *(Macaca fuscata)* have developed and transmitted solitary "play" behaviours of manipulating multiple stones. The way in which these stones are played with also varies from group to group. Likewise, a 23-year observation of white-faced capuchins (*Cebus capucinus*) led by Susan Perry identified social conventions with potentially dangerous side effects (Perry et al., 2011). As well as hand sniffing and sucking of body parts, researchers identified "games" initiated in a play context. The most extreme example of this is "eye-poking" whereby a monkey inserts a partner's finger into his own eye socket up to the first knuckle. Such a game surely carries the risk of damaging the eye and so raises questions as to the function or benefit of such a behaviour. Perry hypothesizes that these dyadic interactions help test and perhaps display the quality of the social relationship. Therefore, a risky tradition reliant on a close social bond serves an important function in another primate species where social bonds are key.

Longevity

By their very definition social traditions are persistent, but the length of this persistence inevitably varies between traditions. Understanding the longevity of a tradition might help us to understand the transmission and function of any socially learned behaviour pattern. There is archaeological evidence that nut cracking in chimpanzees using stone hammers was present over 4,000 years ago in West Africa. Fragments of the same nuts eaten by present day chimpanzees were found on the stone tools. This supports other evidence that the behaviour of nut cracking is a persistent social tradition.

Conversely, some social traditions already described were invented, transmitted and then expired within the time the group was being observed. Susan Perry wrote that, among the wild capuchins that she observed over many years, the most remarkable thing about the seemingly non-adaptive but socially important social customs was the number of apparent extinctions of traditions observed in a relatively short time. For example, hand sniffing died out in several groups after just a few years of observation. Such short-lived traditions may be seen as akin to human fashions and fads in which a behaviour develops among a population and is transmitted enthusiastically for a period of time, before fading quickly. An obvious example of a human fads is fashion in the way we use materials to adorn our bodies. Similar behaviour of adorning bodies with a material has been observed in one of four groups of chimpanzees housed in a sanctuary in East Africa. Specifically, chimpanzees selected a stiff, straw-like blade of grass, inserted the grass into one of their own ears, adjusted the position, and then left it in their ear during subsequent activities (van Leeuwen, Cronin, & Haun, 2014).

Perry speculates that the short life of the capuchin traditions might be due to group instability or the difficulty of preserving traditions that require an understanding of two roles, or due to the death of the initiator of the behaviour. Another possibility is that social traditions with an instrumental function may persevere longer than traditions with a social or normative function. To date there has been little experimental work on investigating what affects the longevity of social traditions. Social learning experiments involving two individuals can only show short-term instances of social learning. A diffusion experimental design, where there are multiple chances for information transfer between numerous individuals, allows for seeded behaviour to be studied over a somewhat longer period of time. Primate diffusion experiments involving artificial fruits have shown relative perseverance of the seeded behaviour. The removal of a reward from a task represents an instrumental context

and so one might expect only the instrumental actions to persevere over generations. Diffusion experiments seeding with functionally irrelevant behaviour is far rarer and thus far only seen with humans. For example, Flynn (2008) investigated children's copying of actions that have no obvious function through a diffusion chain (child A models for child B who then models for child C and so on). The initial child in each chain performed a series of actions on an artificial fruit task in order to retrieve a reward. Some actions were instrumental in removing the reward whereas some actions were functionless. Children showed initial fidelity to the precise action that had the function of removing the reward. However, the actions that did not function to remove the reward were parsed out in the diffusion chains over multiple "generations". These results support the notion that there might be a relationship between a function of a social tradition and the longevity of this tradition. This is an area ripe for further exploration.

Model-based biased transmission

In the previous sections we reviewed tentative evidence that the function of a behaviour or tradition might affect its transmission. These are examples of how social traditions may be shaped by social learning biases or strategies that dictate the circumstances under which primates copy others. These strategies allow an individual to counteract the risk in social learning, of potentially acquiring outdated or maladaptive information. These biases also likely play a crucial role in determining how behavioural variants are spread and maintained at population levels. One social learning bias posits that the identity of the innovator of a particular behavior, or the users of a long-standing behavior, may influence the persistence of a social tradition. Such biases are model-based social learning biases.

Longitudinal observations of the acquisition of tool-based termite fishing in chimpanzees has shown that young females spend significantly more time observing their

termite-fishing mothers than young males. These females successfully termite-fished around two years earlier than young males and the techniques of female offspring closely resembled those of their mothers. The close proximity of the mother and female offspring certainly gave the young females the opportunity to socially learn the behaviour. This observation is based on correlation so inference of causation must be guarded, but it suggests that if two equally viable behaviours were invented by a mother or another individual, the mother's behaviour would more likely be adopted by female offspring, and potentially other members of the group. Increased observation of particular individuals has also been found with capuchin monkeys that attend more to successful conspecifics.

Kendal and colleagues (2015) gave four captive groups of chimpanzees a novel extractive foraging device and tracked the adoption of two methods of reward- retrieval. The groups showed evidence of method preference although every group discovered both methods. Investigating competence and rank, the researchers used statistical models to provide evidence of model-based biases in the transmission of the method choice. Chimpanzees that had not yet had success with the task tended to choose to observe individuals of a higher rank or trained demonstrators (as in two of the groups) more than those of the same rank. However, high-ranking individuals rarely showed fidelity to one method and were not prone to watching social information. The authors speculate that this pattern of copying, biased towards a high-ranking model who does not seem prone to social learning themselves, may explain why high innovation rates among low rank individuals do not generate a correspondingly high frequency of traditions in chimpanzees. Again, this sort of research is in its infancy and is hampered by issues of dominance or monopolization of resources within primate populations.

Migration and Conformity

The pervasiveness of a social tradition may lead individuals to change existing behaviour to that of the majority group behaviour. Such a change represents another example of biased transmission and can be seen as a form of conformity. An effective way of observing conformity in the wild is to track individuals migrating from one group to another. Van de Waal, Borgeaud, & Whiten (2013) presented four groups of wild vervet monkeys with two adjacent trays of maize corn. One tray contained normal tasting corn dyed one colour and another tray contained highly distasteful corn dyed an alternative colour. The monkeys soon learned to avoid the distasteful coloured corn. The trays were removed for several months in which time 10 males moved to a group that preferred the alternative coloured food to that eaten in their original group. When the trays were returned, both now tasted normal. After observing others feeding there, the first choice of seven of these males was for the locally preferred corn which was previously the distasteful option for them. None of the resident males ate the colour corn that was previously distasteful. A further two 'immigrants' adopted the new group's behaviour once higher ranking animals moved away from the preferred food. The only male that continued to eat the same colour as in his original group immediately took the top rank in his new group, a factor that may have influenced his behaviour. Understanding conformity to an individual's new group will add considerably to our understanding of cultural transmission in animals. For example as noted earlier, observations in the wild showing that migrating female chimpanzees assimilate their new group's behaviours (Luncz & Boesch, 2014) might explain the observed maintenance of distinct cultural repertoires in neighbouring communities.

Considering the link between the function of a social tradition and the motivation for conformity is important. For the migrating vervet monkeys, conformity to the new group might represent informational conformity whereby the information provided by the new

group provides environment-specific information about the best food source. Alternatively, the migrants may be more concerned about adopting the behavior of the new group for social reasons such as creating affiliative bonds or adhering to group norms. This is termed normative conformity. Certainly, the one male that maintained his old group norm while becoming the new group's dominant male indicates that there may be something more complex than just informational conformity occurring. Normative conformity is a well-documented human phenomenon. But finding direct evidence for normative rather than informational conformity would, again, be challenging with primate populations.

Fig. 2. *Vervet monkeys eating coloured corn. Here, an infant (left) sits on the colour earlier made distasteful to its mother (before it was weaned), as it eats the colour currently preferred by its mother and the rest of the group. Photo from van de Waal et al. (2013).*

Divergences with Humans

Humans and several other primate species show convergence in (1) group level behavioural differences indicative of social traditions; (2) the ability to socially learn these behaviours; (3) the presence of both instrumental and social traditions; (4) biased transmission of social traditions; and (5) migratory flexible behaviour change allowing behaviour matching with a new social group. With all this convergence, the question remains as to why there is still such an obvious disparity between humans and primates in terms of the breadth, complexity and evolution of social traditions.

While some might define culture as synonymous with social traditions insofar as both display distinctive and persistent socially learned group behavioural traits, human culture possesses characteristics that animal culture lacks. While animal traditions and human culture provide naive individuals with a means of acquiring adaptive behavioural innovations, human culture demonstrates traditions across a richer range of behavioral domains and serves functions never seen in animal traditions. Thus, human culture is divergent from primate traditions, for only humans appear to assimilate socially learned traits that function as markers of shared group membership and result in communal understanding of group-appropriate behaviour.

When research focuses on the function of social traditions, human and animal traditions are seen as more similar than when studies focus on the mechanisms of acquiring social traditions. Emerging research suggests that human culture is dependent on psychological processes that are either absent or severely limited in apes. As previously noted, humans appear to show higher fidelity copying than other primates. This difference, along with other socio-cognitive skills, typically seen in humans but absent in other animals, could have the potential to affect the complexity and efficacy of social transmission of information.

Dean et al. (2012) presented children and captive groups of chimpanzees and capuchins with a multi-step artificial-fruits task, where completion of each of three stages increased reward value. The capuchins and chimpanzees generally struggled to get beyond stage 1, and individuals failed to learn from the few individuals that did reach higher stages. In contrast, the majority of the groups of children reached the final stage and their performance corresponded with a number of other behaviours not seen in the chimpanzees or capuchins. These included high fidelity copying and pro-social behaviour from the model including pro-sociality (reward sharing), communication and active teaching.

This suite of socio-cognitive skills meant that at the group level there was high fidelity copying but also a progression of success on the task. A cycle of high fidelity copying alongside improvement leads to what is commonly known as the ratchet effect, which tends to prevent the slippage of innovations and social traditions discussed earlier. Such a cycle is thought to be responsible for the important human phenomenon of cumulative culture, whereby the complexity or efficiency of cultural traits are enhanced over repeated transmissions. Cumulative culture creates behaviours and technologies that could not have been invented by a single individual in his/her lifetime.

To date, there is very little evidence for cumulative culture in any species besides humans and any evidence is often controversial. When possible behaviour modifications have been identified in the wild these modifications are not always more complex nor more efficient than previous behaviours, nor such that one individual could not have invented them alone. Likewise, direct empirical investigation of cumulative culture in primates has often shown conservatism to original solutions and thus an inability to move to more complex or efficient behaviour. Furthermore there is only very limited evidence that any modifications move beyond what an individual could invent for themselves. Thus to date, substantial cumulative culture appears to be a uniquely human characteristic.

Conclusion

Primate social traditions have been identified in a number of Old-World and New-World monkeys, and in great apes. These animals demonstrate a cognitive capacity for social learning as well as the presence of distinct and persistent inter-group behavioural differences. Such traditions share many features with human traditions such as variation in function, longevity, biased transmission and plasticity, although the exact nature of these features may also often differ between humans and other primates. There remains a huge gulf between primate traditions and human culture due to the volume, persistence and cumulative nature of human culture, but the evidence for primate culture reviewed here indicates that human culture did not spring out of nowhere; it has substantial roots in earlier phases of primate evolution

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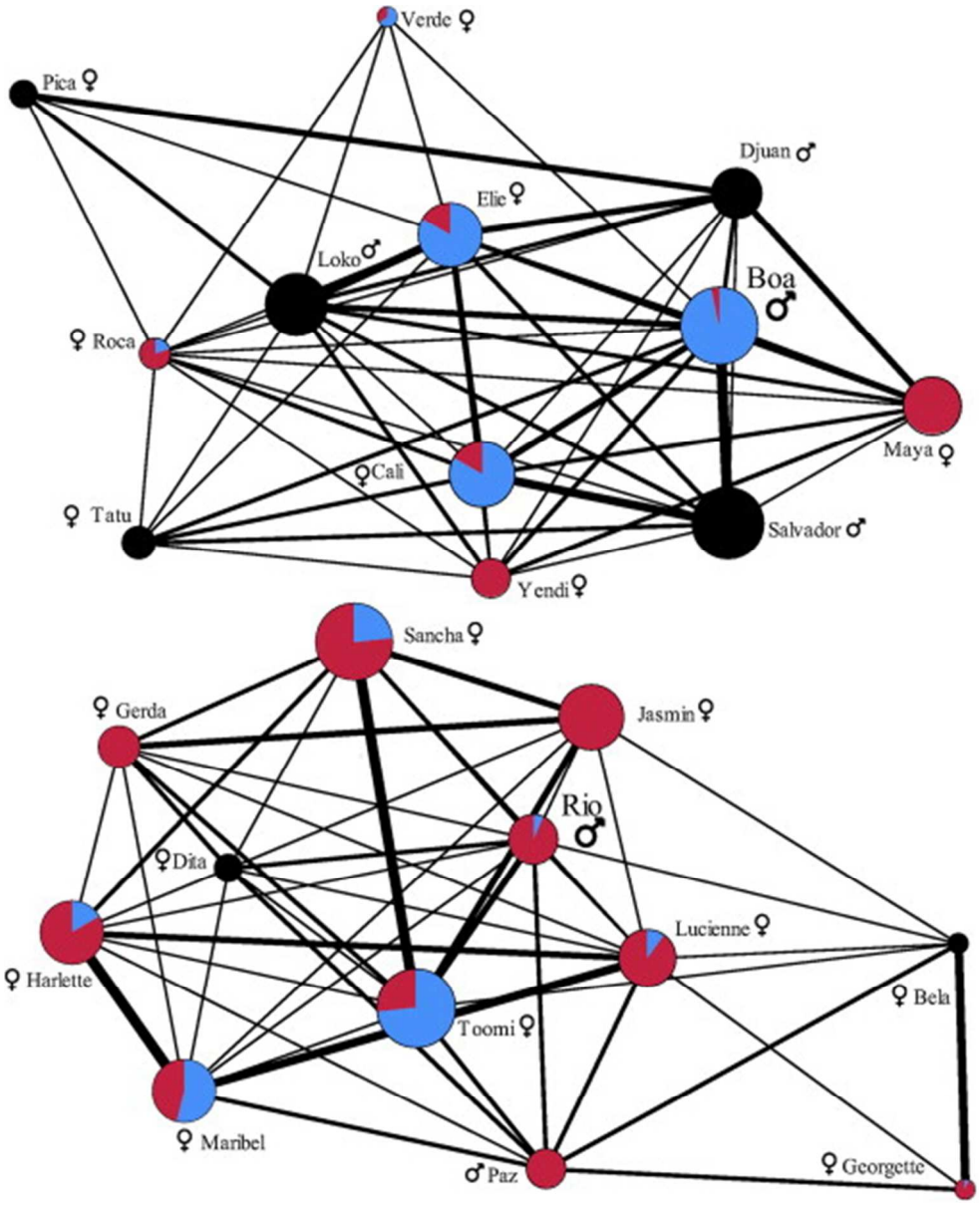

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113x139mm (113 x 113 DPI)

Fig. 2. Vervet monkeys eating coloured corn. Here, an infant (left) sits on the colour earlier made distasteful to its mother (before it was weaned), as it eats the colour currently preferred by its mother and the rest of the group. Photo from van de Waal et al. (2013).
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